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The distribution of the montane palaeogenic element in the South African invertebrate fauna

INTRODUCTION

The palaeogenic invertebrates are among the most archaic animals in our fauna, and they contribute greatly to its temperate facies. Their antiquity is revealed by a discontinuous distribution in more than one zoogeographical region, and by their confinement, within the Ethiopian Region, to South Africa. These elements are mostly relict, primitive types belonging to ancient groups usually undergoing regional evolution along distinctive lines. Their concentration in South Africa is a well-known feature, especially since it is part of a clearly-defined pattern in the southern hemisphere, which shows a stock of ancient invertebrates and plants zoned in the southern parts of the continents. The purpose of this paper is to outline the distribution of certain of the best known or most characteristic of the South African palaeogenic invertebrate groups, and to attempt some generalizations concerning the distribution of this faunal component.

The distribution of a number of these palaeogenic elements is related to a certain range of temperature and humidity conditions peculiar to montane areas, and it is some of these elements that will be considered here. Included are silvicolous groups, groups with aquatic immature stages in montane streams, and groups with terrestrial immature stages occurring in alpine grassland or macchia. The distribution of the deserticolous palaeogenic elements is quite different and must be the subject of a separate study.

Many invertebrate groups are still poorly known and badly collected, and all too frequently have not been reviewed or monographed. Hence this study is inadequately documented. Also, it is absolutely certain that data concerning examples used in this paper will have to be modified to accord with the results of future collecting, as our knowledge of most of these groups is very superficial. Indeed some of the distribution maps presented below show possibly better the spheres of activity and dispersal of staff during field trips from the South African and Natal Museums! These deficiencies are inevitable at this stage in the exploration of our fauna, and it is considered that they do not invalidate the general conclusions drawn below. Further examples of distribution patterns in palaeogenic groups can be abstracted from papers listed in the references; it will be seen that they agree in large measure with the patterns mapped in Figs. 1–7.

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Distribution Patterns of some Palaeogenic Groups

The distribution of these invertebrates has been plotted by means of a $\frac{1}{4}$° square grid system on outline plotting maps supplied by the Government Printer, Pretoria.

In Fig. 1 the Limpopo and Great Fish Rivers are indicated by dotted lines, the Great Escarpment in the eastern part of South Africa by a heavy broken line, and the northern limit of the geological province of the Cape Fold Mountains by a continuous heavy line. This map shows the distribution of blepharocerid flies. There is one genus in South Africa, *Elporia* Edwards, evolved from a generalized Paltostomine and related to Palaearctic and Neotropical genera. The immature stages are torrent-dwellers, living in clear, well-oxygenated mountain streams, and this makes them eminently suitable for zoogeographical studies. The family is an old and rather isolated one. In the map the localities on the Cape Fold Ranges are distinguished by hollow squares from those of the Eastern Highlands, namely Basutoland, the entire Drakensberg Escarpment, the Amatola Range and the Eastern Plateau Slopes (for an explanation of this term see Wellington, 1946). *Elporia* extends from the Cape Peninsula to the northern end of the Eastern Transvaal Escarpment. Its species fall clearly into two assemblages, one on the Fold Mountains and the other in the Eastern Highlands, no species crossing the Fish River Valley. The Cape species are most numerous in the south-west, and there is one outlying species (related to a Cape species) on the Kamiesberg which is not a part of the Fold System (Barnard, 1947). The species of the Eastern Highlands fall into three groups (Stuckenberg, 1955, 1961b); (*a*) those of the Basutoland Drakensberg Highlands, with outlying populations or related species on scarps in the Natal Midlands, Zululand and Griqualand East, six endemic species in all; (*b*) two species on the Amatola Range, having affinities with those of the Basutoland Drakensberg Highlands; (*c*) those of the Transvaal Escarpment, and the Plateau Slopes around Barberton, four endemic species derived from the Basutoland Drakensberg Highlands. One species is common to *a* and *c*.

Fig. 2 shows the distribution of the Lucanid genus *Colophon* Gray (based on Brinck, 1956). This genus is endemic to the ranges of the south west Cape, where it has undergone intensive speciation (Barnard, 1929). Its twelve species are all apterous summit-dwellers of unusually restricted distribution, and the immature stages live in soil. *Colophon* is placed in the subfamily Lampriminae which includes otherwise only genera from South America and Australia, as well as one in Baltic amber of lower Oligocene age (see Brinck, *op. cit.*).

Fig. 3 indicates the known distribution of three genera of Diptera. *Pachybates* Bezzi (*a*) and *Trichacantha* Stuckenberg (*b*) are the only endemic genera of Rhagionidae in the Ethiopian Region (Stuckenberg, 1960a). They are related and possess a curious combination of primitive and specialized anatomical features. Their nearest relative seems to be *Atherix* Meigen, a genus with a wide range in the northern hemisphere and occurring also in South Africa as a palaeogenic element. The larvae of *Pachybates* and *Trichacantha* are aquatic, living in clear mountain streams. *Pachybates* is known only from the south-west Cape, *Trichacantha* from the forested belt between Knysna and Port Elizabeth, but it is certain that they have a wider range over the Fold Mountains than is indicated. *Peringueyomyina* Alexander (*c*) is the only African member of the primitive family Tanyderidae. The single species, *P. barnardi* Alexander, is known from a few localities in the south-west Cape; it occurs near montane streams in the sandy margins of which its larvae live (Wood, 1952). Its affinities are uncertain, though Wood (*op. cit.*) observes that the immature stages are very like those of the Nearctic *Protoplasa* O.– S.

Fig. 4 indicates the distribution of the Megaloptera, an ancient order which in Africa is entirely confined south of the Limpopo. All its members are aquatic in the immature stages, preferring mountain streams. There are four endemic genera in two families (Barnard, 1931, 140). Corydalidae are represented by the monotypic *Chloroniella* E.– P. (*a*) confined to a small area within the South-West Cape; *Platychauliodes* E. P. (*b*) has five described species distributed on the mountains of the south-west Cape and in the Knysna area; *Taeniochauliodes* E. P. (*e*) has a single species with a wide range, known from many localities in the south-west Cape and distributed along the Fold Mountains as far east at least as Storms River it occurs also in Natal on the Drakensberg and on the outlying Karkloof Range

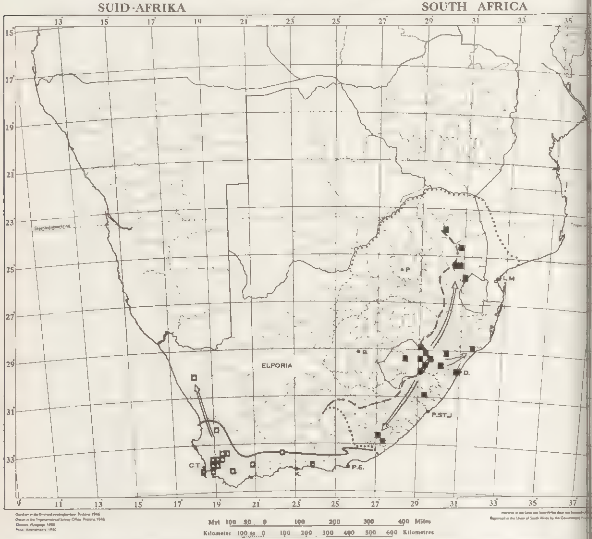
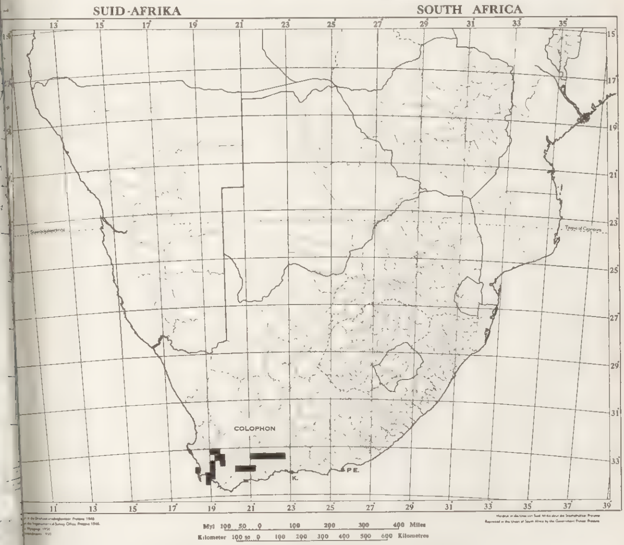


Fig. 1: The distribution of Blepharoceridae (Diptera). There is one genus, *Elporia* Edwards. Localities in the Cape Centre are indicated by hollow squares The dotted lines trace the courses of the Limpopo and Great Fish Rivers, the continuous heavy line marks the northern limit of the Cape Fold Belt and the broken heavy line the approximate position of the eastern part of the Great Escarpment. There are three foci of speciation in the Eastern Highlands Centre.

(Crass, 1949). The family Sialidae is represented by *Leptosialis* E.– P., whose single species, *africana* E.– P. (*c*) occurs in the south-west Cape, in the eastern Cape in the Kokstad-Franklin districts and Amatola Range, and in Natal on the Escarpment (Barnard, *op. cit.;* Crass *op. cit.*).

Fig. 5 shows the known distribution of four genera that have related forms in South America or Australasia, or both. The single South African species of the Dermapteran genus *Esphalmenus* Burr, *E. peringueyi* (Bormans), is known from the localities marked *g* (Hincks, 1957, 57 58). It is strictly montane and has been found in the Basutoland highlands, southern


SUID-AFRIKA
SOUTH AFRICA
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COLOPHON
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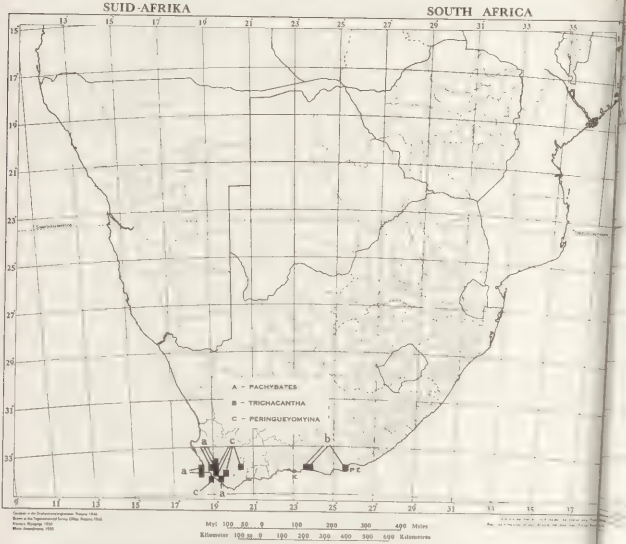
Fig. 2: The distribution of *Colophon* Gray (Coleoptera: Lucanidae).

Drakensberg, and in the Cape Fold Mountains westward to the Cape Peninsula. The only other members of the genus are five species in temperate South America. *Afrothaumalea* Stuckenberg (*c*), a monotypic genus of Nematocerous Diptera described only in 1960, is related to *Austrothaumalea* Tonnoir of temperate South America and Australasia. At present it is known from a female specimen found on the crest of the Natal Drakensberg and a male from the south-west Cape (Stuckenberg 1960b, 1961a). The immature stages of Thaumaleidae are known to live in seepage or thin films of water. *Atherimorpha* White (*e*) is an interesting


SUID-AFRIKA
SOUTH AFRICA
A - PACHYBATES
B - TRICHACANTHA
C - PERINGUEYOMYINA
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Kilometer 100 50 0 100 200 300 400 500 600 Kilometres

Fig. 3: The occurrence of three genera of Diptera, the Rhagionids *Pachybates* Bezzi (*a*) and *Trichacantha* Stuckenberg (*b*), and the Tanyderid *Peringueyomyina* Alexander (*c*).

genus of Diptera with a number of South African species (Stuckenberg 1956a, 1961b); they are poorly known, being seldom collected. At least two species occur in the Basutoland-Drakensberg Highlands, an undescribed species has recently been found on the Zuurberg, and two species are on the ranges of the south-west Cape. The genus otherwise inhabits south-east Australia, Tasmania and temperate South America. In some respects the South African species show affinities with the genotype from Tasmania. *Arthroteles* Bezzi (*a*) is an endemic genus locally derived from *Atherimorpha*. It is strictly montane, with a species in

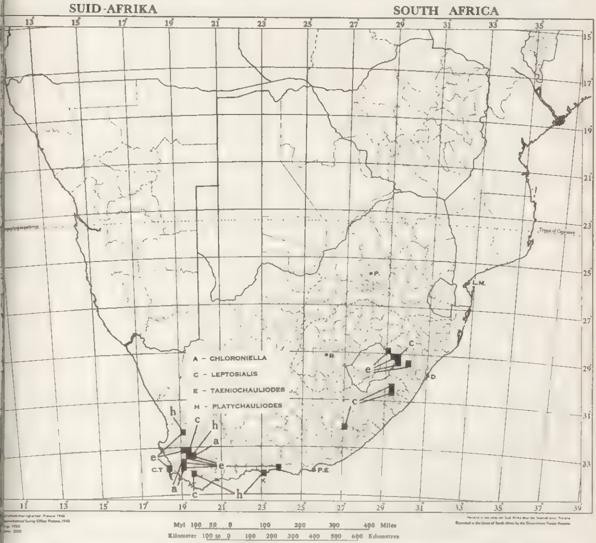

Fig. 4: The distribution of Megaloptera. The Corydalidae are represented by *Chloroniella* E. P. (*a*), *Platychauliodes* E.– P. (*b*) and *Taeniochauliodes* E.– P. (*e*); there is one genus of Sialidae, *Leptosialis* E.– P. (*c*).

the Natal Drakensberg and two, possibly three, in the south-west Cape (Stuckenberg, 1956b) The immature stages of *Arthroteles* and *Atherimorpha* are unknown. Both genera seem to have a preference for macchia vegetation, especially in the Cape, and possibly have terrestrial larvae.

Fig. 6 shows the distribution of the South African Onychophora, *Opisthopatus* Purcell and *Peripatopsis* Pocock (based on Brinck, 1957, and augmented by data supplied by Dr. R. F. Lawrence). On the map the Cape and the Eastern Highlands species are distinguished.

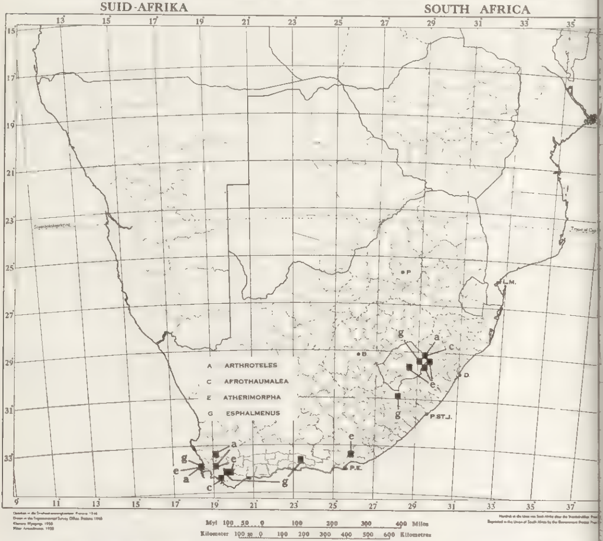

Fig. 5: The distribution of *Esphalmenus* Burr (Dermaptera); and three genera of Diptera, (*c*) *Afrothaumalea* Stuckenberg (Thaumaleidae), (*e*) *Atherimorpha* White (Erinnidae) and (*a*) *Arthroteles* Bezzi (Erinnidae).

The genus *Peripatopsis* has its centre of distribution in the Cape Fold Mountains where there are nine endemic species; one species, *P. moseleyi* (Wood-Mason) extends from the eastern Cape to Natal, occurs in forests of the Natal Midlands and on the Amatola Range, and crosses the Fish River Valley to only the eastern end of the Fold Belt. *Opisthopatus* is an eastern genus with two species; *roseus* Lawrence seems very restricted, being known only from the highlands in the Harding District, but *cinctipes* Purcell has the widest range of all, occurring in forest on the Transvaal Drakensberg, at numerous localities in Natal, Zululand and Pondo-

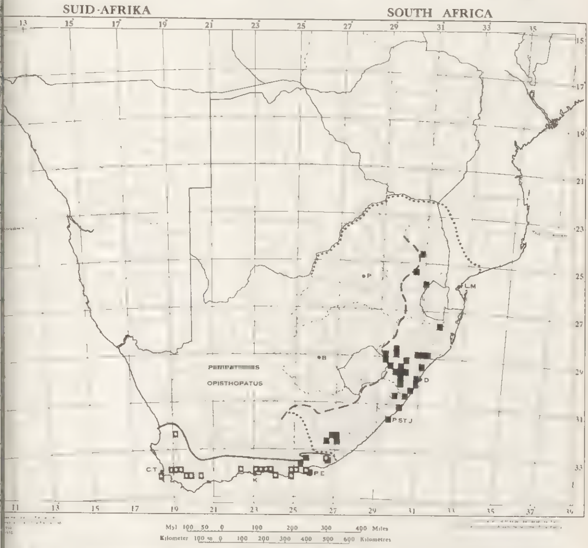

Fig. 6: The distribution of Onychophora. There are two genera, *Opisthopatus* Purcell and *Peripatopsis* Pocock. Hollow squares indicate localities for species endemic to the Cape Fold Mountains.

land, from sea-level to the upper limit of montane forest at about 5,000 ft., and like *moseleyi* also at the eastern end of the Fold Belt. In many respects the distribution of *cinctipes* is a typical of the faunal constituent being examined here, since this species is ecologically much more tolerant, living near sea-level and in places under subtropical conditions. In view of this it is surprising that it has not crossed the Limpopo Valley. The affinities of the

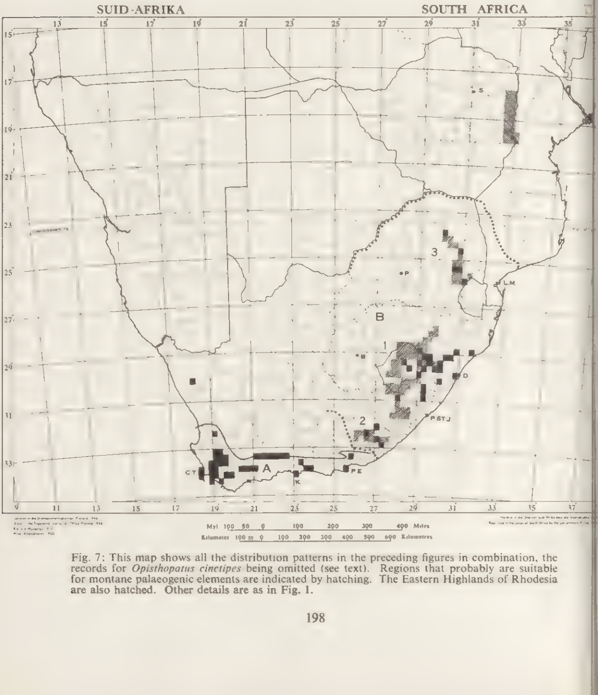

Fig. 7: This map shows all the distribution patterns in the preceding figures in combination, the records for *Opisthopatus cinctipes* being omitted (see text). Regions that probably are suitable for montane palaeogenic elements are indicated by hatching. The Eastern Highlands of Rhodesia are also hatched. Other details are as in Fig. 1.

South African Onychophora are latitudinal and not longitudinal, *Opisthopatus* being related to the South American *Metaperipatus* Clark, and *Peripatopsis* to *Paraperipatus* Willey of Notogea (see Brinck *op. cit.*).

A Synopsis of the Patterns shown by these Groups

In Fig. 7 all the distribution patterns are shown together, the records for *Opisthopatus cinctipes* being omitted. Probable localities in the Eastern Highlands, where at least some of the aforementioned groups are likely to occur, are shown by hatching. Suitability of a locality was decided on the basis of field experience and a consideration of the following factors:

- (*a*) Altitude: at Cathedral Peak in the Natal Drakensberg the distribution of the faunal components has been investigated; here the lowest limit to which the palaeogenic elements occur is about 7,600 ft., except those groups with aquatic larvae which range down to 4,500 ft. where stream conditions permit.
- (*b*) Relief: relative relief is obviously important, since prominent topographical features tend to have a higher rainfall than surrounding lower country; cases in point are the Amatola and Zuurberg Ranges.
- (*c*) Aspect: east-facing slopes are more suitable because of their higher rainfall.
- (*d*) Rainfall: from a consideration of distribution records it seems that the 35-in. isohyet is of at least local significance.
- (*e*) The distribution of the Stormberg Volcanic Series: this series of lavas is responsible for the altitude and relief of the highlands of Basutoland and the fringing Escarpment, and of the high country between Barkly East and Elliot to the south of that territory. The lower level of the series is never below 5,000 ft. (du Toit, 1926). In the western part of Basutoland there is approximate coincidence of the fringe of this series with the 35-in. isohyet. In its central part Basutoland has been deeply eroded by the Orange River drainage whose valleys lie in rain shadow.

The overall distribution of the palaeogenic elements considered here thus includes the ranges of the Cape Fold Mountains and the Eastern Highlands as far north as the end of the Transvaal Drakensberg. This pattern seems characteristic also of other palaeogenic groups such as Plecoptera (Balinsky, 1956; Barnard 1934; and unpublished data), the Odonata *Chlorolestes* Sélys, *Ecchlorolestes* Barnard and *Presba* Barnard (Brinck, 1955), various genera of Ephemeroptera (Barnard, 1932, 1940; Crass, 1947), and genera of Myriopoda and Opiliones (Lawrence, 1953). It fits as well primitive groups which have entered South Africa from the north sufficiently recently to be represented still by relict species on tropical mountains or highlands in Africa, examples being carabid beetles of the genus *Plocamotrechus* Jeannel (Basilewsky, 1958) and turbellarians of the genus *Cura* (Marcus, 1955). In many respects the same pattern is shown by members of the Cape Flora (see Weimarck, 1941), a resemblance in distribution due perhaps in some cases to a direct association with that Flora, but in other cases to a dependence on a similar set of ecological requirements. In fact it seems that this pattern is widely applicable, and thus worth a brief examination in more detail.

The range of the montane palaeogenic elements falls into two parts, for which the terms *Cape Centre* and *Eastern Highlands Centre* are suggested (indicated in Fig. 7 by A and B respectively). This is not a complete division as it is not relevant to all groups.

The Cape Centre: This comprises the Fold Ranges of the Cape System, the approximate northern limit of which is shown in Fig. 7 by the heavy line. The ranges fall into two groups (du Toit, 1926; King, 1942), a slightly older western group tending north-south, and a more elongate southern group trending slightly south of east. These groups intersect in a complex manner in the south-west Cape. Within the Cape Centre distribution is determined largely by rainfall consequent upon relief and aspect, and the effects of rain shadow are profound.

The zones favourable for montane palaeogenic elements are restricted and narrow, and generally only the summits and seaward slopes of the ranges are suitable. In places, as in the Tsitsikamma area, these elements are found in forests on the coastal plateau or in river gorges seaward of the mountains. Species in some genera, for example *Peripatopsis* (Brinck, 1957) and *Ecchlorolestes* (Brinck, 1955), show a tendency to fall into eastern and western assemblages within the Cape Centre. The western group of Fold Ranges and the region in which the two groups intersect are in the winter rainfall zone, and it is here that there is the extraordinary concentration of palaeogenic elements that has attracted so much attention. For a high proportion of elements the eastern limit within the Cape Centre is Algoa Bay. The eastern extremity of the Fold Belt, comprising the Zuurberg and country around and to the east of Grahamstown, is apparently much poorer in palaeogenic elements, and its significance will be discussed below.

The Eastern Highlands Centre: As can be seen in Fig. 7, this falls roughly into three subcentres.

(1) The Basutoland—Drakensberg Highlands and Eastern Plateau Slopes: an extensive area suitable for palaeogenic elements but as yet little explored. Basutoland and the high country to the south, built by the massive pad of Stormberg lavas, are occupied today by alpine grassland; the Cape macchia is represented but is not a dominant floristic component (Weimarck, *op. cit.*). At the highest altitudes there is a noticeable impoverishment of the flora which shows as well many morphological changes in response to cold, poor soil and altered composition of sunlight (Schelpe, 1946). In the Natal Drakensberg, palaeogenic elements with aquatic immature stages, such as Blepharoceridae and Megaloptera, are to be found as far down as 4,500 ft. where stream conditions are suitable, and upwards right to the extreme headwaters where these rise on the lip of the Escarpment, sometimes showing species-succession with increasing altitude (as in Blepharoceridae). On the Plateau Slopes these stream-breeding groups are widely scattered but in a more or less definite pattern, being almost invariably distributed along scarps bordering elevated remnants of the Miocene Peneplain, cut by the cycle of erosion initiated by uplift in the mid-Miocene (see King and King, 1959).

Among grassland insects there are relatively few palaeogenic elements up to about 7,000 ft. at Cathedral Peak in the Drakensberg, and most of the species are common Midlands ones or range even further afield, but above about 7,600 ft. a change is evident. Flowering plants become more abundant, especially *Scabeus* and many species of *Helichrysum;* with increasing altitude the number of the lowland insect species decreases precipitously and there is a concomitant acceleration in the number of endemics. Close to the crest of the Escarpment, above 9,000 ft., both fauna and flora are greatly reduced in species, but these are now almost all endemic and many belong to palaeogenic groups.

Montane forest cannot be dealt with at length here; reference should be made to Lawrence (1953) and Acocks (1953). It has its upper limits at about 5,000 ft. in the Drakensberg and at numerous localities on the Plateau Slopes. This forest is now scattered in many relict patches, but the conclusion is inescapable that these were formerly much more extensive and commonly continuous with one another. The distribution of the forest element generally is likely to be best understood on the basis of the probable original extent of forest as shown in Acocks' (1953) Map No. 1.

(2) The Amatola Range: This is built of Karroo rocks, and is an outlier of the high country at the southern end of the Drakensberg. The Amatolas probably became an independent physiographic entity after the mid-Miocene, as they are isolated by the valleys of the Great Fish and Great Kei Rivers which cut back and became deeply incised in soft Ecca Shales after regeneration following elevation in the mid-Miocene and in subsequent

cycles. Nevertheless this Range must have been a feature of fair relief before that time as its summits are well above the present-day level of the Miocene Peneplain.

(3) The Eastern Transvaal Subcentre: As far as is known at present, this is restricted in extent, occupying the Transvaal Escarpment as far north as the Tzaneen area, and the elevated country around Barberton. Only stream-breeding and silvicolous palaeogenic elements occur here.

The significance of these subcentres for speciation varies from group to group. In Blepharoceridae speciation has been very active. This may have been due to a more complete subcentral division of the mountain stream biome by the absence of a well-defined Escarpment in the Middleveld area (see King, 1942); here the Miocene Peneplain of the Highveld slopes to the Lowveld, though with much local relief. Whether this is true for other stream-breeding groups is uncertain. In silvicolous groups many examples could be provided of closely allied species in the forests of Natal and the Eastern Transvaal subcentre, though in other groups the same species occur throughout. Acocks (1953) distinguishes the forests of the Eastern Transvaal subcentre and those of Natal as different floristic types, Inland Tropical Forest and Temperate Forest respectively, so there may be an ecological basis for speciation within these subcentres.

Shown also in Fig. 7 are the Eastern Highlands of Southern Rhodesia. These mountains are known to have some palaeogenic elements that have obviously entered from the south, though the number is small. Examples have not been provided by the groups considered above, but are to be found in *Lampromyia* Macquart (Stuckenberg, 1960a) and *Chlorolestes* Sélys (Pinhey), 1951).

Intervals in the Pattern: At the extreme eastern end of the Fold Belt there is an area transitional between the Cape and Eastern Highlands Centres. This comprises mainly the Zuurberg and mountains around and to the east of Grahamstown. At present it is isolated climatically, on the north side by the dry Fish River valley, and to the south-west by an arid zone extending from the interior to the shores of Algoa Bay. There are two areas of maximum precipitation, one on the Zuurberg and the other to the east of Grahamstown, in neither case exceeding 35 in. p.a. The Uitenhage basin, which lies between Port Elizabeth and the Zuurberg, formerly had a rugged topography, but this was submerged beneath marine deposits laid down by a marine transgression which penetrated far into the basin during the lower Cretaceous (du Toit, *op. cit.*). During the Tertiary a second but less extensive marine transgression deposited the Eocene-Pliocene Alexandria formation over part of the Uitenhage basin and eastward termination of the Fold Belt, and must have affected the suitability of the region for palaeogenic elements. This transition zone is relatively depauperate, most of the Cape palaeogenic invertebrates stopping west of Port Elizabeth, and few of the Eastern Highlands elements crossing the Fish River. It is transitional for example in Onychophora (Fig. 6), certain Ephemeroptera (Crass, 1947) and probably Plecoptera (Balinsky, 1956; and unpublished data). In some respects the Amatolas are part of the transition region as well, as there is a number of examples of groups which extend from the Cape Centre no further north than the Amatolas. A good example is provided in Opiliones: in the genus *Larifuga* a series of species extends from the Cape Peninsula to the Amatolas, while the related genera *Larifugella* and *Adaeulum*, have an eastern distribution, just crossing the Fish River valley to the south and extending to the Eastern Transvaal subcentre in the north (Dr. R. F. Lawrence, *personal communication*). The Great Kei River valley, deeply incised, and occupied by Valley Bushveld (Acocks, *op. cit.*), clearly is a barrier comparable to the Great Fish. In Acocks' map of Veld Types (Government Printer, Pretoria, 1951) macchia (subdivided as False Macchia, No. 70) is shown to extend from the west over the transition zone at the end of the Fold Belt and to be checked by the arid Fish River valley and its Valley Bushveld (No. 23). Evidently there is a natural floristic boundary here as well.

The most significant interval of all is the Limpopo valley, which delimits in a decisive manner the northern distribution of many palaeogenic invertebrate groups. This is an ancient trough since Jurassic and Cretaceous faults border it on the south against the Zoutpansberg. It interrupts widely the Escarpment and its Mopani and Bushveld are almost a complete barrier to stream-breeding and silvicolous palaeogenic elements occurring on the Transvaal Drakensberg. This low-lying tract has been a highly efficient ecological barrier far back into the Tertiary.

CONCLUSIONS

As a result of more extensive collecting in recent years it has become apparent that many of the montane palaeogenic invertebrates formerly known from the south-west Cape have a wider distribution. Many of these have been found in mountainous parts in the east and north-east of South Africa. The distribution pattern shows two main centres, a Cape Centre and an Eastern Highlands Centre, the latter with three sub-centres, as described above. The Cape Centre is the richer of the two in species, frequently richer in genera, rarely in families, amongst the examples considered and among others in the literature. This richness in species, and therefore probably the greater number of genera, is clearly due to the presence of an extraordinary combination of factors promoting speciation in the Cape Centre. Among these factors might be mentioned the antiquity of the landscape, the folds being post-Ecca and pre-Cretaceous, with a recrudescence of faulting in mid-Cretaceous (King, 1942); the varied nature of the topography, mountain ranges of considerable relief though relatively low altitude rising abruptly from a flat coastal plain or intermontane valleys, incised transversely by deep poorts and longitudinally by old established drainages, features which initiate allopatric speciation; the floristic trichotomy of forest, macchia and karroo vegetation, three competing floras, the macchia often being associated with montane palaeogenic elements and having undergone frequent rearrangement in response to climatic change (Weimarck, *op. cit.*); and the climate, characterized by winter rainfall in the south-west and more or less perennial rains east of the Gouritz River, the zones of high rainfall being confined to the summits and sea-facing slopes of the Fold Mountains, with marked rain-shadow effects in the intermontane valleys.

It is the opinion of the author that the Cape Centre is not to be regarded because of its faunistic wealth as the node from which palaeogenic elements have spread to the mountains in the north-east. The occurrence of these elements in the Basutoland-Drakensberg Highlands is instead considered an original feature of a very old distribution pattern. This opinion is based on the following observations. Firstly, these highlands are an ancient physiographic entity (see King, 1942). They owe their existence to the cap of Stormberg lavas which are resistant to water erosion. The lavas were extruded in the early Jurassic, and after being folded to the east in the Natal Monocline, must have been subjected to river erosion, at which time the present drainage pattern evolved and when the Drakensberg Escarpment must first have been formed. This Escarpment has thus been continuously present since late Jurassic times. It was unaffected by the rise of the Cretaceous seas which drowned parts of the Cape Centre. In fact, the Basutoland Highlands were one of the few remaining areas of high ground suitable for palaeogenic elements, persisting at the close of the planation of the continent in the mid-Miocene. Secondly, the last occasion when these Highlands were sufficiently continuous with the Fold Belt to share a common fauna must have been before the separation of the Amatola Range (i.e. mid-Miocene at latest). It must also have been during a time when conditions were favourable for a wide distribution of temperate montane forms, which was probably not during a cycle of planation but during or subsequent to a period of elevation of the continental rim relative to sea-level. The latest available opportunity for this would seem to have existed in the late Cretaceous (see Dixey, 1955, and further references given by him).

It may be objected that this view cannot be correct since the Cape Flora, although possessing many features in its overall distribution pattern very like those outlined for palaeogenic invertebrates (see Weimarck, *op. cit.*), obviously is centred in the south-west Cape. The evidence for this location is impressive; according to Weimarck (p. 98) the Cape has four endemic families, 212 endemic genera and 3,536 endemic plant species of the Cape element, whereas only 347 species, not all endemic, are found in the Drakensberg. Probably the answer is to be found in the former distribution of forest, which is a potent competitor of the macchia vegetation. In Acocks' Map No. 1 forest is shown to have formerly restricted the macchia to the group of western Fold Mountains, the region regarded as the centre of distribution of this Flora. Its representatives on the Drakensberg have probably been derived from there during periodic contractions of the forest during climatic changes, and doubtless by means of chance immigration as well. In the south-west Cape the macchia underwent an explosive local evolution, far exceeding that of the fauna, but this must be seen as a special feature of the area.

This is essentially a preliminary study. A better understanding of the distribution of the montane palaeogenic elements can be possible only after a great deal of further collecting and taxonomic endeavour. More ecological investigations are also required as these must play a major rôle in the elucidation of factors controlling the dispersal of our palaeogenic invertebrates, notably as regards stream-breeding insects since we are concerned in their case with a zoogeography of immature stages. It seems safe to predict that more of these animals will be found in the Eastern Highlands, especially Basutoland and the Drakensberg. The prospect is exciting.

SUMMARY

The palaeogenic invertebrates are among the most interesting and distinctive animals in the South African fauna. This paper is an attempt to investigate the distribution of those that are confined to mountains. The distribution patterns of certain genera of Diptera, the Megaloptera, Onychophora, some Coleoptera and a Dermapteran are used as examples. The patterns show two main areas occupied by these invertebrates, a *Cape Centre* (the Cape Fold Mountains, especially in the south-west Cape) and an *Eastern Highlands Centre* (the Amatola Range, Basutoland, Natal Drakensberg, Eastern Plateau Slopes and Eastern Transvaal Escarpment). At the eastern end of the Fold Belt and southern end of the Eastern Highlands is a transition zone between the Centres, created partly by an arid tract of marine sediments extending inland from Algoa Bay and by ecological conditions unfavourable to montane forms in the Great Fish and Great Kei Valleys. The Limpopo Valley delimits the palaeogenic elements in the north, and is a major ecological barrier. It is considered that this pattern is a primitive one.

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DISCUSSION

Prof. Balinsky: The speaker mentioned that the paleogenic fauna is composed of three elements, namely silvicolous groups, groups with aquatic larvae and groups of the Cape macchia. He gave us a clear idea of the first two but not of the third.

Dr. Stuckenberg: This was for lack of time. Some are mentioned in the written paper.

Dr. Harrison: Amongst aquatic groups we have found montane species extending to the Drakensberg and Nyasaland, and, amongst Mayflies and Chironomids, even to the mountains of Abyssinia. Collecting is often very sparse but the distribution follows a pattern very similar to that shown by Dr. Stuckenberg.

Dr. Bigalke: It is interesting that there are even mammals such as the Bontebok and Bloubok, which are endemic and restricted to the South-west Cape.

Dr. Stuckenberg: I feel I should emphasize a fundamental distinction here. Practically all the vertebrates in the South-west Cape can be derived from tropical fauna; but the significance of these paleogenic invertebrates is that they are limited to the tips of the southern continents. They have few near affinities and such as they have are latitudinal not longitudinal. In Africa they have no northern relatives from which they could be derived.